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Ecological studies of Collembolan populations in a pine forest soil

I. — The life cycle and population dynamics of *Tetracanthella sylvatica* Yosii

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INTRODUCTION

Recently ecological studies of Collembola have received increasing attention because of their importance in soil formation and litter decomposition.

Laboratory studies have shown the life history for many species and the effect of environmental factors upon the animal under experimental conditions. Ecological studies in the field have demonstrated the numerical fluctuations and the qualitative aspects of life history, but little is known about which factors govern these population and life history phenomena, it is a necessary preliminary to obtain information on the life cycle and to estimate population parameters such as birth and mortality rates which attribute to the fluctuation and abundance of the population.

This work forms part of an investigation of the ecology of collembolan populations in a pine forest and is mainly an account of the life cycle and population dynamics of *Tetracanthello sylvatica* Yosii.

I. — STUDY AREA

The study was carried out in a Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) forest at Kamigamo Experimental Station of Kyoto University, being situated about 12 km north of Kyoto City (35°. 04′ N. and 135°. 43′ E.).

The sampling plot was located on the top of a hill being about 130 m in altitude. The sampling area was dominated by *Pinus densiflora*, mixed with *Chamaecyparis obutusa* Endl. The scrub layer was moinly dominated by *Pieris japonica* D. Don, *Euria japonica* Thumb. and *Lyonia elliptica* Okumura.

The soil profile under this plot showed no well developed structure and with no transition zone between the organic and mineral soil layers. The L layer was about 1 cm deep, consisting mainly of pine needles. The F layer was about 2-3 cm in thickness. The H and A layers were poorly developed and the boundary between these layers was not recognizable. The B layer was below 3-5 cm in depth, consisting of heavy clay soil.

II. — ASPECTS OF CLIMATE

The main features of the climate of Kamigamo Experimental Station during the study period are given in Fig. 1. The mean air temperature ranged from 3.4° C (January) to 28.5° C (August). The soil temperature at 10 cm depth ranged from 4.7° C (January) to 26.7° C (August.) The annual precipitation and evaporation were 1683 mm and 985 mm respectively.

During the study period, the pattern of seasonal changes in soil and air temperature did not differ greatly from year to year. The temperature was maximum in August, declining towards autumn and winter and reached its minimum in January. The seasonal changes in evaporation were similar to those of temperature. The seasonal pattern of precipitation was similar to that of temperature and evaporation, but precipitation in summer 1973 was exceptionally low.

III. — SAMPLING AND EXTRACTION METHODS

The sampling plot measured 10 × 10 m², being divided into twenty sub-plots of 1 × 5 m². During the period from July 1971 to July 1975, sampling was done at about monthly intervals.

Samples consisted of soil cores each 25 cm² in surface area and 4 cm deep (100 cc in volume). The number of soil cores taken on each sampling occasions is shown in Table I.

For the study of vertical distribution, sampling was made at monthly intervals, from October 1972 to August 1973 and on two further occasions, July and August 1974. The samples consisted of eight soil cores, each being 25 cm² in area and 4 cm deep. The soil core was cut into four layers, each 1 cm thick and of volume of 25 cc. Soil arthropods were extracted by a high gradient canister extractor (MACFADYEN 1961) at a constant temperature of 35° C (temperature in the extractor). The period of extraction was six days. The extracted animals were collected into a solution of picric acid. The identification, counting and measurement were undertaken under binocular microscope with micrometer.

IV. — RESULTS

1. Seasonal changes in soil water content.

Soil water content was measured on each sampling occasion and expressed as ratio of water to dry weight of soil. The results are shown in Fig. 2. Soil water content was low during spring and summer, except in spring 1972 and in summer 1974 and high during autumn and winter. The drought of the soil during spring and summer is explained by the high evaporation during these periods.

2. **Population density.**

The mean density of *T. sylvatica* per 1 m² is given in Table I together with standard errors. During the study period, the population density ranged from 0 to 16 880 with a mean of 3 550 per m². Maximum density occurred in winter, being 1 769, 8 036, 16 880 and 13 095 per m² in 1971, 1972, 1973 and 1974 respectively.

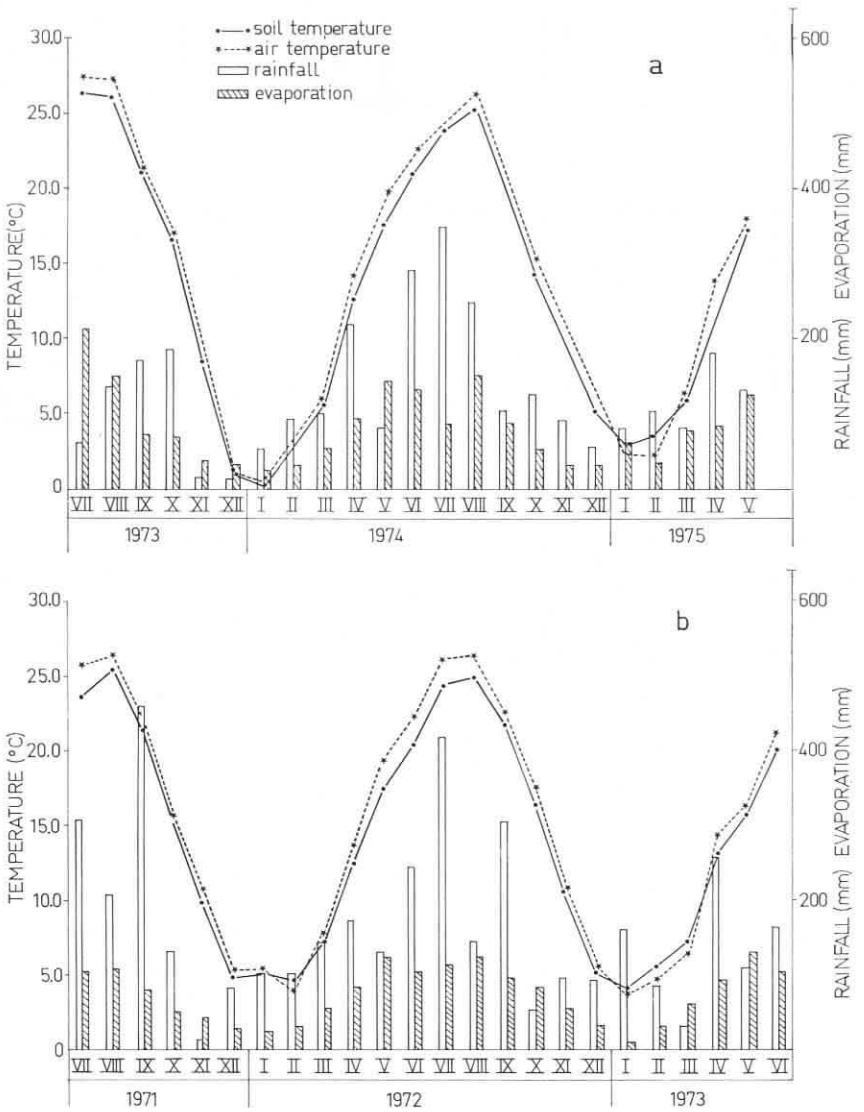

FIG. 1. — Climatic feature of Kamigamo Experimental Station during July 1971 to July 1975.

TABLE I

The number of soil cores sampled, together with the date, mean population density of *T. sylvatica* per 1 m² and standard errors

Date	1971 3/VII	3/VIII	9/X	12/XI	15/XII	1972 25/I	23/II	20/III	22/IV	10/V	20/VI
Number of units..	12	12	12	12	12	12	12	12	12	12	12
Density per 1 m²..	0	0	440	886	766	1769	1020	1454	1733	440	1066
Standard error....	0	0	284	312	318	942	424	753	681	217	471
Date	1972 7/VII	1/IX	29/IX	28/X	1/XII	24/XII	1973 28/I	1/III	3/IV	14/V	10/VI
Number of units..	18	20	18	25	22	20	20	20	20	20	20
Density per 1 m²..	0	324	1311	4716	8036	4080	8176	5240	2660	560	1920
Standard error....	0	215	564	1346	1244	1058	3654	940	983	256	816
Date	1973 9/VII	25/X	3/XII	1974 12/I	13/II	11/III	17/IV	14/V	16/VI		
Number of units..	20	17	17	15	18	17	15	15	17		
Density per 1 m²..	560	3976	4880	16880	7956	4118	4086	2187	1176		
Standard error....	326	1538	1661	4180	1812	1253	943	909	244		

Date	1974 26/VII	30/VII	30/IX	31/X	30/XI	30/XII	1975 30/I	8/III	3/IV	3/V	30/V	1/VII
Number of units.....	15	20	20	20	15	18	19	19	20	15	20	20
Density per 1 m².....	1714	421	3020	8240	7740	13095	8441	10084	5828	3337	2920	2180
Standard error.....	400	165	1210	3196	2608	6484	2492	2733	1586	1353	808	856

The minimum density occurred in mid summer, being 0, 0, 560 and 421 per m^2 in 1971, 1972, 1973, and 1974 respectively.

The species showed one annual peak occurring in mid winter and the pattern was similar from year to year.

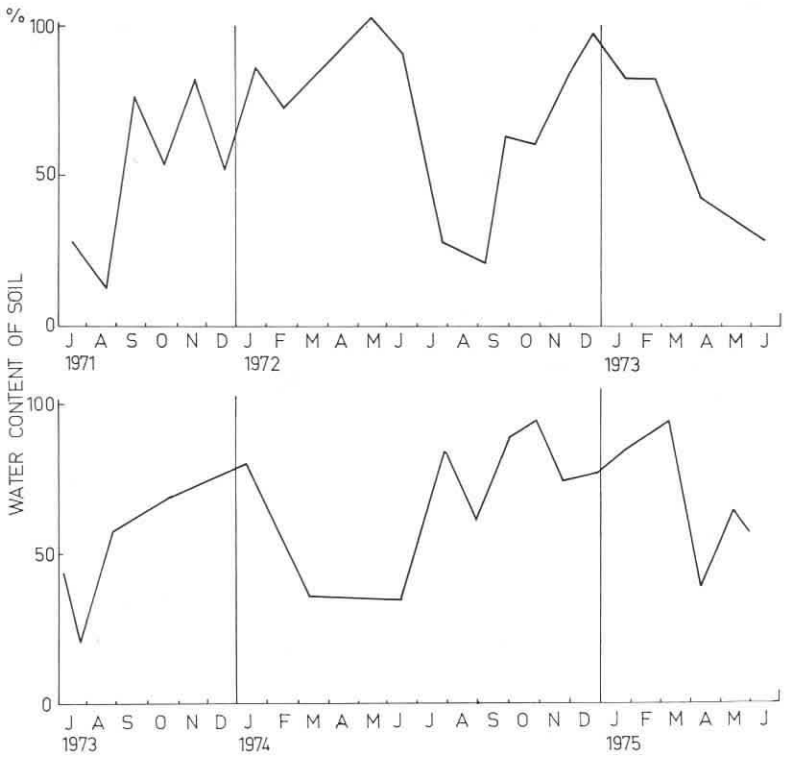
%
100
50
0
WATER CONTENT OF SOIL
J A S O N D J F M A M J J A S O N D J F M A M J
1971
1972
1973
100
50
0
J A S O N D J F M A M J J A S O N D J F M A M J
1973
1974
1975

FIG. 2. — Seasonal changes in the water content of soil. Water content of soil is expressed as the ratio of water to dry weight of sample.

3. **Life cycle of Tetracanthella sylvatica.**

Collembola have no marked metamorphosis and they grow by a series of moults which continued throughout life, so it is difficult to interpret the age of individuals in terms of instar classes for the natural population.

Therefore, for the study of age structure, the individuals were divided into nine size classes using body length.

The adults were separated from juveniles by using the difference of pigmentation, for the samples collected during the period from July 1971 to June 1974. For the samples collected from July 1974 to June 1975, the individuals were separated into adult and juvenile by observing the genital area. The first method of separation was verified by the second method.

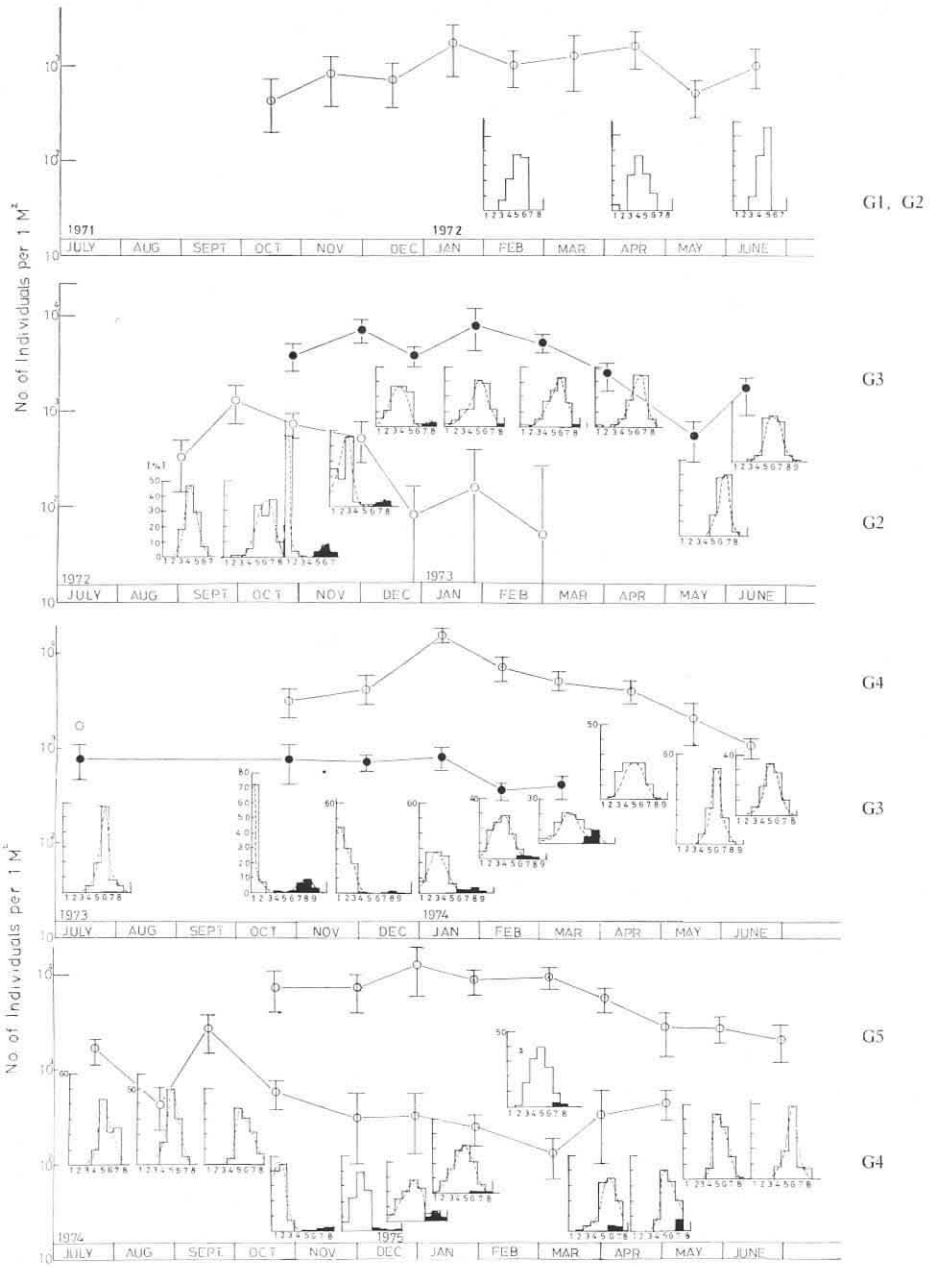

FIG. 3. — Seasonal changes in the body length distribution and the mean population density per m² for each generation of *T. sylvatica*. The individuals sampled are grouped into nine size classes, i.e. 1st (< 0.5), 2nd (0.5-0.625), 3rd (0.625-0.75), 4th (0.75-0.875), 5th (0.875-1.00), 6th (1.00-1.125), 7th (1.125-1.25), 8th (1 25-1.375) and 9th (> 1.375 mm). G.1, G.2, G.3, G.4 and G.5 indicate the 1st, 2nd, 3rd, 4th and 5th generation respectively.

a. *Seasonal changes in age-structure.*

The monthly changes in size structure are shown in Fig. 3 by frequency distributions of the size classes. The number in each size class is given as a percentage of total number sampled on each occasion. The mean density per 1 m² is also given for each generation with standard errors. The large percentage of the first size class in October indicates that recruitment occurred mainly during October. During the recruitment period, the size distribution of juveniles was separed from that of adults, then overlapped with that of adult during late winter and spring. During summer the size distribution consisted of adults, being unimodal in shape.

b. *Growth analysis.*

In this species, the recruitment period was limited to short time periods as indicated in previous section.

Accordingly, the growth curve of individuals can be obtained by following the subsequent growth in the mean body length of individuals for a given generation. The mean body length of individuals was plotted against the sampling date, with 95 % confidence limits. The growth curve for each generation is shown in Fig. 4. The pattern was not different for the four generations and was represented by a S curve.

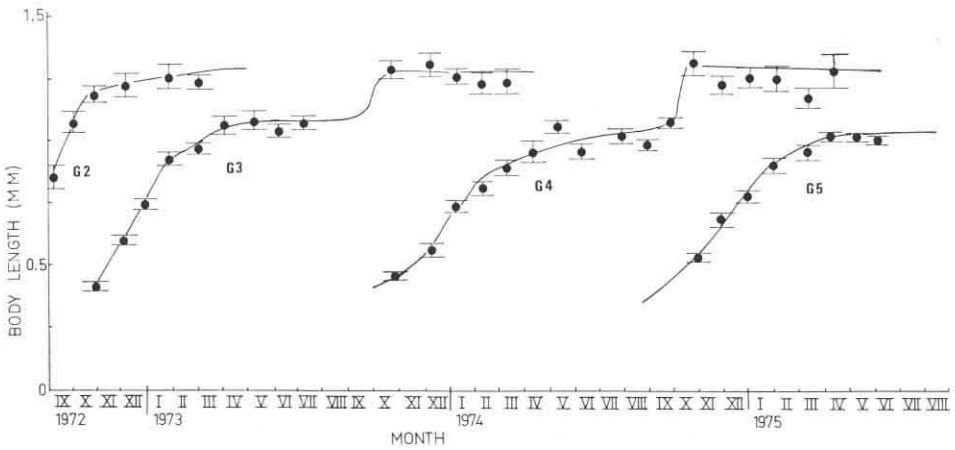

FIG. 4. — Growth curve for each generation of *T. sylvatica*. The mean body length of individuals is plotted against sampling date with 95 % confidence limits.

Egg and juvenile stage.

In the absence of data on eggs, the age structure and the degree of maturity of animals provided information on the oviposition and egg period. On 29 September 1972, the population consisted of the prematured adults individuals (Fig. 5 B) and on the next sampling occasion (28 October 1972) the population consisted of newly hatched and adult individuals, indicating that oviposition and hatching took place during the period and the period of egg stage was shorter than one month.

The mean body length of newly hatched individuals was about 0.4 mm.

Thereafter individuals grew rapidly during autumn and winter

The mean growth rate during these period was about 0.12, 0.13, and 0.13 mm per month for 3rd, 4th and 5th generations respectively.

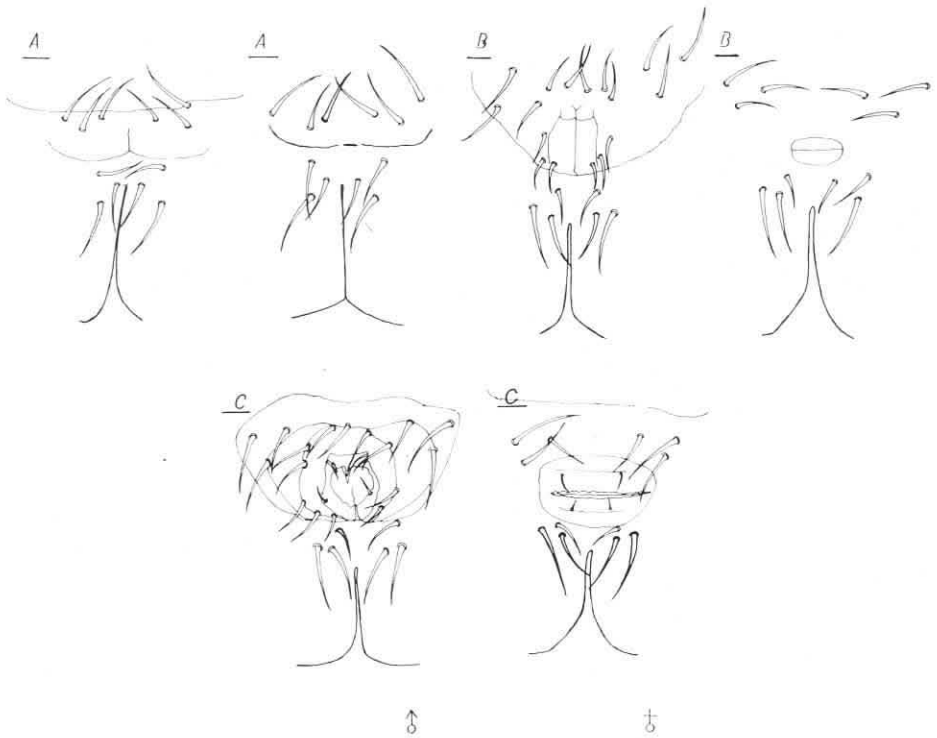

FIG. 5. — Area of genital orifice of *Tetracanthella sylvatica*. A, B and C represent the old juvenile, pre-adult and adult stages respectively.

In late spring, growth began to decline and was arrested during summer. Body length attained nearly the same as that of adults by late spring. At the begining of summer, the population consisted of several development stages as distinguished by the genital morphology: the most developed individuals were in stage A (Fig. 5 A) being provided with a groove which was distinctly extended longitidially or transversely, but for individuals being in the early stages, the genital opening was very faint or not developed. In late summer, the population mainly consisted of juveniles in stage A. The decrease of variation in developmental stage occurred during summer.

Adult stage.

The mature individuals appeared in October with newly hatched individuals and sexual maturation was syncronized in all individuals collected on 30 September 1974, indicating that sexual maturation was completed between late summer and early autumn. Over the recruitment period, the sex ratio

TABLE II

Sex ratio of *T. sylvatica* on different sampling ocasions
Sex ratio was calculated as total females to total adults

Date	1972 29/IX	1974 30/IX	31/X	30/XI	30/XII	1975 30/I	8/III	3/IV	3/V
Sex Ratio.....	0.48	0.49	0.57	0.86	0.63	0.83	0.83	0.92	0.78

was nearly 1 : 1 ($P < 0.001$.) (Table II). After recruitment, there was a consistent excess of females in population (Table II). At adult stage, the body length female was longer than that of male and the difference was significant ($P < 0.05$). (Table III). Thus the sudden increase in mean body length was due to a higher proportion of females in the population.

TABLE III

Difference between body length of female and male of *T. sylvatica* over the recruitment period

Date	29 septembre 1972	30 septembre 1974
Body length (male)...	1.097 mm	1.020 mm
(female).....	1.244 mm	1.123 mm
Probability.....	0.001	0.001

4. **Population dynamics.**

a. *Vertical distribution.*

The vertical distribution of *T. sylvatica* was studied on two occations by taking 20 vertical cores. Each core was taken to 8 cm depth and divided into two layers each being 4 cm in thickness. The results are shown in Fig. 6.

The higher proporation of individuals occurred in the upper 0-4 cm layer. This concentration of individuals in the surface layer may have been due to the soil structure properties in the study area. Namely, below the humus layer, the soil profile changed abruptly into mineral soil layer which had a very compact structure.

Thus the vertical distribution of this species was limited to the organic soil layer.

The vertical distribution within the 0-4 cm layer was studied by taking further vertical cores. The seasonal changes in vertical distribution within the 0-4 cm layer are shown also in Fig. 6. During the recruitment period, both adults and newly hatched juvenile occurred only in the 0-1 cm layer, suggesting that oviposition took place in the surface layer. After recruitment, *T. sylvatica* apparently migrated into deeper layers throughout the spring and summer.

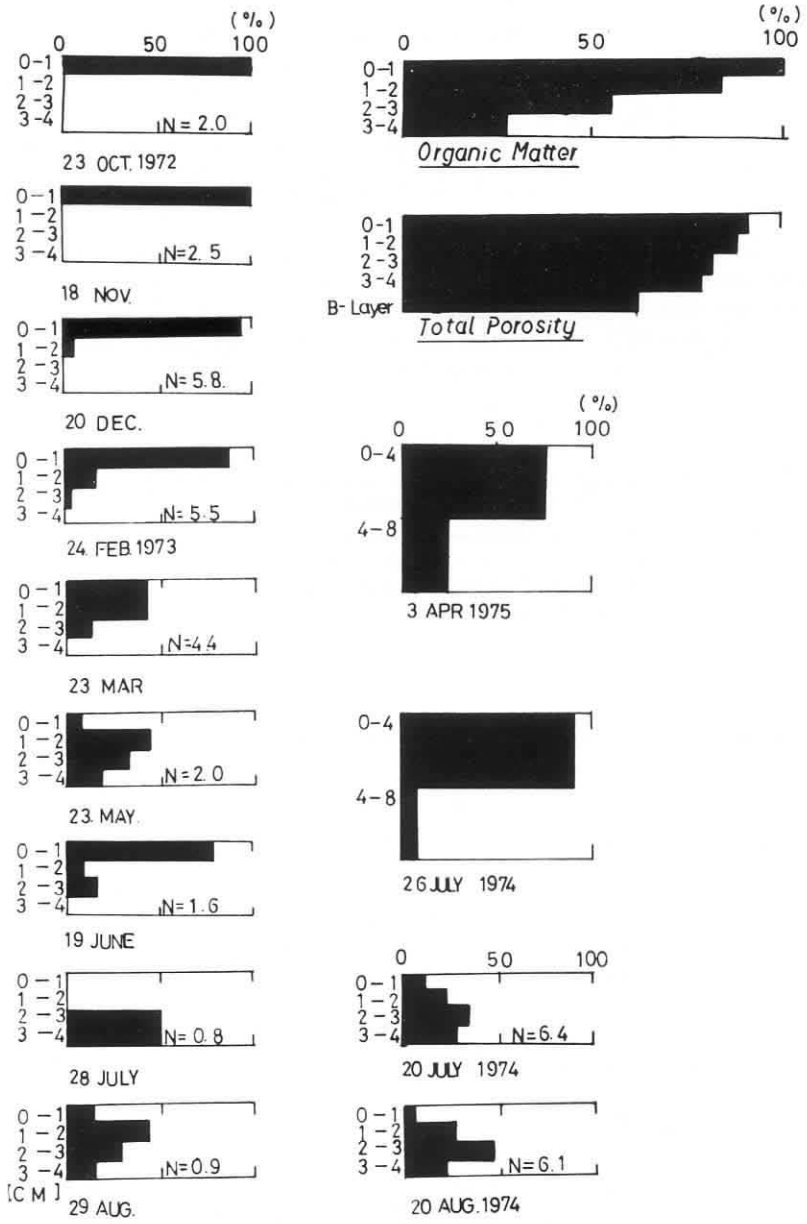

FIG. 6. — Vertical distribution of *T. sylvatica*. The number of animals present in each sub-horizon is expressed as a percentage of the total population on each sampling occasion. N indicates the number per 100 cc core.

b. *Horizontal distribution.*

The distribution pattern of *T. sylvatica* was examined by the $\overset{*}{m} - \overline{m}$ regression method (IWAO 1968). The relationship between mean ($\overline{m}$) and mean crowding ($\overset{*}{m}$) is expressed by the formula:

$$\overset{*}{m} = \alpha + \beta\ \overline{m}$$

where the intercept (α) indicates whether the basic component of the distribution is a single individulas or a group of individuals, and the slope (β) indicates how the basic components are distributed over thespace. Using the data obtained by monthly sampling, the estimates of mean crowding ($\overset{*}{X}$) and mean ($\overline{X}$) were calculated by the following formulas (LLOYD 1967).

$$\overset{*}{X} = \frac{\sum_{j=1}^{q} X_j\ (X_j - 1)}{\sum_{j=1}^{q} X_j} \qquad \overline{X} = \frac{\sum_{j=1}^{q} X_j}{q}$$

where q is the number of soil core sampled, X_j; the number of individuals in the j th core. The $\overset{*}{m} - \overline{m}$ regression was obtained by using the sample estimates of mean crowding and mean.

For the first years samples: $\overset{*}{X} = 0.22 + 3.24\ \overline{X}$ ($r^2 = 0.84$)
For the second years samples: $\overset{*}{X} = 1.46 + 3.09\ \overline{X}$ ($r^2 = 0.83$)
For the third years samples: $\overset{*}{X} = 2.69 + 1.90\ \overline{X}$ ($r^2 = 0.94$)

The value of β was 3.24, 3.09 and 1.90 for first, second, and third years samples respectively. The value of α was not large enough to show the presence of a colonial component although the values were all positive.

The approximately linear relationship of mean crowding to mean density over the study years suggests that the distribution pattern is mainly determined by the heterogeneity of habitat factors such as the soil porosity, depth of organic soil layer, which is fairly stable over the year.

c. *Survivorship curve.*

The survival of individuals of each generation can be followed for as long as recruitment does not occur.

In each year, recruitment was complated by late winter, and then the population size subsequently decreased. The survival curve was obtained for each generation from the population decrease. The results are shown in Fig. 7.

The mortality in the juvenile stages mainly occurred during autumn, winter and spring. During these periods, the trend of population decrease was nearly exponential, indicating that the survival rate did not differ between the different size classes.

The mortality during late juvenile to adult was very low. During late spring and summer, the population showed a temporary drop in numbers but it recovered in the autumn. Hence, the population decrease is attributable to other reasons rather than to mortality. The followng factors are consi-

dered; first, the sampling errors because of the high degree of aggregation; second, the majority of the population migrated deeper than 4 cm and third, the animals were inactive and they were not extracted.

Sampling errors were large but the difference for the population decrease was significant. The vertical distribution showed that animals migrated into deeper layers during these periods as shown in Fig. 5. The distribution range of this species is limited to the organic soil layer. Therefore, the vertical migration alone may not account for the decrease in numbers. The decline was limited to the period of drought, when the soil condition was unfavorable, and very shrivelled individuals were collected during these periods, suggesting that this species became inactive in responce to unfavorable conditions, especially soil drought.

After recruitment, the adult individuals suddenly decreased in number and disappeared by spring. Thus the overlapping of adults individuals of different generations did not occurred during the study period.

d. *Recruitment and mortality.*

The pattern of mortality of *T. sylvatica* was represented by juvenile mortality occurring during autumn, winter and spring and adult mortality occurring after the recruitment period (Fig. 7).

Mortality rate in the juvenile stage during autumn winter nad spring and recruits entering each generation were estimated by the regression method of RICHARD and WALOFF (1954). This method assumes that the mortality rate does not differ between the different age classes and the population has a fairly synmetrical peak. The trends of a population can be represented by the following equation:

$$\log y = \log n + x \log k.$$

where y is the density on day x, n is the total number of recruits entering a generation, k is the fraction of the population surviving day. The regression was calculated for each generation. The estimated recruits were 1 758, 19 762, 36 812, and 28 184 per m for 2nd, 3rd, 4th and 5th generation respectively. The number of recruits was remarkably low in the 2nd generation. The estimated mortality during the juvenile period was 38, 91, 95, and 92 % for 2nd, 3rd, 4th and 5th generation respectively.

It is notable that the mortality rate was remarkably low in 2nd generation which had a low density.

V. — DISCUSSION

During the study period, *T. sylvatica* showed a pattern of autumn, winter and spring growth, arrest during summer and recruitment during autum. The life cycle pattern was not different from year a to year. It is well known that univoltine species have a diapause to escape unfavorable conditions and to synchronize the life cycle to the environment. ANDREWARTH (1956) defined diapause as a stage in the development of certain animals during which morphorogical growth and development is suspended or greatly retarded. According to this definition, the

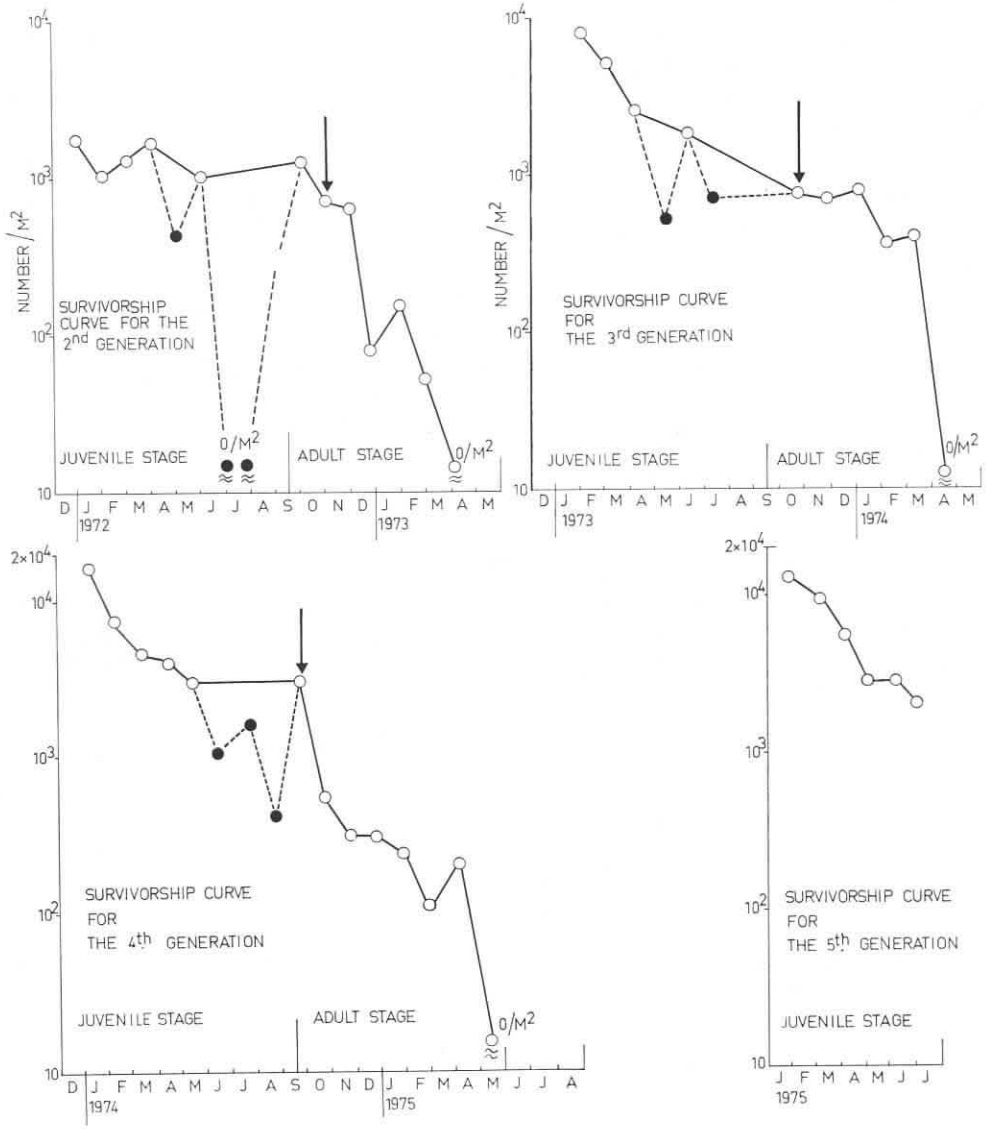
NUMBER / M2
SURVIVORSHIP CURVE FOR THE 2nd GENERATION
JUVENILE STAGE
ADULT STAGE
0/M2
D J F M A M J J A S O N D J F M A M
1972
1973
SURVIVORSHIP CURVE FOR THE 3rd GENERATION
JUVENILE STAGE
ADULT STAGE
0/M2
D J F M A M J J A S O N D J F M A M
1973
1974
SURVIVORSHIP CURVE FOR THE 4th GENERATION
JUVENILE STAGE
ADULT STAGE
0/M2
D J F M A M J J A S O N D J F M A M J J A
1974
1975
SURVIVORSHIP CURVE FOR THE 5th GENERATION
JUVENILE STAGE
J F M A M J J
1975

FIG. 7. — Survivorship curve of *T. sylvatica*. Arrows indicates the oviposition period.

arrest of growth of *T. sylvatica* during summer can be regarded as diapause. In this species, although the developmental stage was different among individuals in early summer, all individuals became adult during the autum; syncronization was thus affected by the arrest of growth during summer.

Generally soil collembola require high humidity (usually above 89 % R. H. CHRISTIANSEN 1964) for their survival. Drought is an important mortality factor for collembolan populations and obviously attributed to the population fluctuations. The

most noticeable feature of the survivorship curve of *T. sylvatica* is that mortality was less affected by the drought during the summer, even in 1973 when drought was severe. The low mortality of *T. sylvatica* may be attributable to diapause during summer.

Adaptation to escape unfavorable conditions have been observed by some workers. MATSUMOTO & SAITO (1926) observed that *Onychiurus watanabei* Matsumoto and *O. matsumotoi* Kinoshita became inactive in responce to high temperatures during summer and entered into aestivation in their nests. Similar behaviour was found in *Subisotoma variabilis* Gisin by POINSOT (1969). This species became inactive under drought conditions and was capable of resisting in a state of anhydration form.

The shrivelled individuals of *T. sylvatica* were similar to this. CASSAGNAU & RAYNAL (1964) found the occurrence of morphologically variable forms in *Hypogastura tullbergi* Schaeffer under high temperatures, distinguishing this phenomenon from diapause and defined it as « écomorphose ». But these adaptation for unfavorable conditions are not common in collembola.

Apart from this adaptation, as an ecological adaptation, most species of collembola have evolved the ability to migrate.

Recently VANNIER (1970) showed that downward migration of Isotomidae took place as soon as the soil water potential reached a permanent wilting point for plants. A vertical migration was observed in *T. sylvatica* during the summer. In the same study area, other species also showed vertical summer migrations, but the mortality of these species was high compared with that of *T. sylvatica* (unpublished data TAKEDA) suggesting that diapause was much more important. The vertical migration is an important adaptation to escape the unfavorable conditions, but the survival value depends upon soil structure. As in this study area where the soil structure is poorly developed, the survival value of vertical migration seems to be low when drought is severe as in 1973.

The fluctuations in numbers of adults and old juveniles was relatively stationary during the study period (Fig. 8). The steady population density may be caused by the following:

(1) the mortality occured mainly during autum, winter and spring when soil condition were not unfavorable for the survival of the population, and during those periods population density was regulated in density dependent manners.

(2) the individuals which survived during those period were less affected by unfavorable conditions, especially soil drought during summer, because of diapause and vertical migration. The effect of density dependent regulation thus maintained during old juvenile and adult stage.

The life cycle pattern of this species may de advantageous in habitats where drought regularly occurs during the summer, but in habitats where soil conditions are favorable throughout the year, a univoltine life cycle may be disadvatageous in competition with other species having several generations each year, because of low reproductive capacity.

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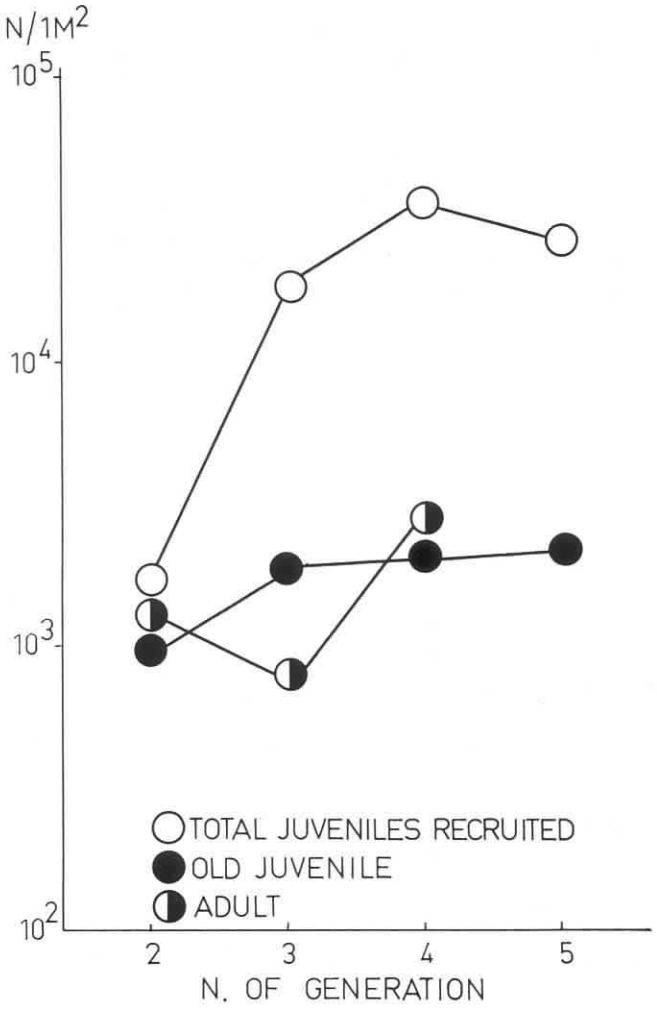

FIG. 8. — Fluctuation in numbers of adults, old juvenile and total juveniles recruited to the population of *T. sylvatica*.

SUMMARY

1. Monthly sampling over a four year period from a pine forest soil near Kyoto in Japan gave information concerning the life cycle and population dynamics of *Tetracanthella sylvatica* Yosii. (Collembola; Isotomidae).

2. This species had one generation per year and the life cycle was represented by autum, winter and spring growth, diapause during summer, and recruitment during autumn.

3. The pattern of seasonal fluctuations in numbers was not different from year to year. This species showed one annual peak occurring mid-winter.

4. The seasonal changes in vertical distribution were studied and it was found that oviposition took place in the surface layer, and the juvenile individuals migrated into deeper layers during spring and summer.

5. The distribution pattern was examined by using the mean crowding — mean regression method, and it was found that this species had an aggregated distribution.

6. The population dynamics were studied for five generations. The survivorship curve was represented by the exponential decrease of the number of juveniles during autumn, winter and spring, low mortality during summer, and a sudden decrease in number after recruitment.

7. During the study period, the numbers of adults and old juveniles were relatively stationary.

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